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# Pollen Dispersion Of Some Forest Trees

*by*

*Jonathan W. Wright*

Northeastern Forest Experiment Station

Ralph W. Marquis, Director

Upper Darby, Pa.

Forest Service, U.S. Dept. of Agriculture

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# CONTENTS


| | Page |
|---|---|
| INTRODUCTION | 1 |
| METHOD | 5 |
| Pollen collection | 6 |
| Calculations | |
| Regression equations & neighborhood size | 10 |
| Pollen trajectories with rate of fall & wind velocity the controlling factors | 12 |
| Weather data | 13 |
| RESULTS | |
| Elm | 13 |
| Ash | 15 |
| Poplar | 16 |
| Douglas-fir | 18 |
| Spruce | 19 |
| Apple | 19 |
| Pinyon | 20 |
| True cedar | 21 |
| FACTORS THAT INFLUENCE DISPERSION DISTANCE | |
| Wind velocity & direction | 26 |
| Topography of the land | 28 |
| Diameter & rate of fall of pollen grain | 28 |
| Turbulence of the atmosphere | 29 |
| Height of pollen source | 31 |
| POLLEN DISPERSION & RACE FORMATION | 32 |
| SUMMARY | 37 |
| LITERATURE CITED | 39 |

# POLLEN DISPERSION OF SOME FOREST TREES

by

Jonathan W. Wright, *geneticist*[1]

*Northeastern Forest Experiment Station*
*Forest Service, U.S. Dept. Agriculture*

## INTRODUCTION

THE DISTANCE THE POLLEN of forest trees travels is of practical and theoretical importance not only in tree breeding, but also in silviculture. For example, one way to produce elite or hybrid tree seed where vegetative propagation is impractical is by the establishment of "seed orchards" or natural-crossing plots. The success of such orchards will depend partly on the pollination habits of the clones used.

In silviculture, these pollination habits may find usefulness as a guide in cutting, to determine the spacing of seed trees to be left to insure adequate natural regeneration.

Pollen-dispersion distance is a relatively unappreciated factor in the formation of local and geographic races

[1] STATIONED AT THE MORRIS ARBORETUM, PHILADELPHIA, PA., IN COOPERATION WITH THE UNIVERSITY OF PENNSYLVANIA.

of forest trees. Recent genetic work has shown that formation of races, especially of animals, is conditioned not only by different selection pressures[2] in various parts of the population, but also by the need for isolation between parts of the population. This is true whether the races are natural, having been formed in past ages, or are man-made as the result of mass selection.

The pollen dispersion of several species was studied by the author between 1944 and 1947 at West Lafayette, Ind., and at Philadelphia, Pa. The results of these studies show that the distances that tree pollen travels are generally much shorter than previous theoretical studies have indicated. The studies also indicate that species differ greatly in the distances their pollens travel.

Past studies of pollen dispersion may be divided into four groups: (1) empirical studies of long-range dispersion from unknown pollen sources; (2) empirical studies of short-range dispersion from known sources; (3) empirical studies of seasonal fluctuation in pollen frequencies (particularly of pollens causing hayfever) at one or more stations; and (4) theoretical studies involving known rates of pollen fall in still air, rate of air movement, observation on diffusion in liquids, etc. The author's studies belong primarily to the second group.

Among those who have made studies of long-range pollen dispersion from unknown sources are Rempe (22)[3], Meier and Artschwager (18), Erdtman (10), and Dengler and Scamoni (6). These workers have found pollen--sometimes in quantity--at considerable distances from the nearest possible source, as much as 14,000 feet above the ground and in the middle of the North Atlantic. In none of these studies was the source frequency (which may be in the billions) determined.

To the second group belong those studies based on the incidence of pollen or of cross-pollination at varying distances from known sources. A number of such studies, as well as studies on the spores of fungi and ferns, have been summarized by Wolfenbarger (26). In predominantly ento-

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[2] THE PRESSURE EXERTED BY THE ENVIRONMENT FOR OR AGAINST A CHANGE IN THE GENETIC CONSTITUTION OF A POPULATION.

[3] UNDERLINED NUMBERS IN PARENTHESES REFER TO LITERATURE CITED, PAGE 39.

mophilous species such as cotton, grape, radish, beans, and tomato, the practical limit of pollen dispersion has been found to vary from 60 to 600 feet (26). Using red-leaf varieties of cotton planted next to green-leaf varieties, Brown (4) reported that natural crossing diminished from 5.6 percent to zero in 40 feet and from 14.8 percent to zero in 400 feet in two different experiments. Pope and others (21) found that isolation barriers of 12 rows of corn reduced the natural crossing between test varieties of cotton by about 50 percent, and that natural crossing diminished from 20.36 percent at the source to 0.02 percent at 4,200 feet from the source. Bateman (1) reported a rapid decrease in natural crossing in radish and turnip from 0 to 160 feet from the source; beyond 160 feet he found a small--but constant--amount of natural crossing.

In anemophilous species the pollen is subject to somewhat greater dispersion. Haber (12), studying the isolation distances necessary for seed plantings of corn, found that there was heavy contamination of one variety by the other at distances up to 115 feet, light contamination from 115 to 300 feet, and very little contamination beyond 380 feet. Bateman (2) found that the amount of contamination in corn decreased from 70 percent at 2 feet to 1 or 2 percent at 50-75 feet; he also studied pollen dispersion of corn, finding that the frequency at 80 feet was less than 0.02 percent of the frequency at the source. Jensen and Bøgh (16) found smaller rates of decrease with increasing distances from the source for several crop plants in Denmark; at 2,000 feet from the source the pollen frequencies were 8 to 15 percent of the source frequencies. Peculiarly, they found the dispersion distances to be nearly as great on days of low average wind velocity (7 miles per hour) as on days of high average wind velocity (12 miles per hour).

Pollen dispersion has also been studied in a few woody species. In hazel (22) the frequency at 400 feet from the source is only about 1 percent of the source frequency. In Persian walnut also there is a marked decrease in deposition with increasing distance from the source, and deposition is negligible at 2,600 feet (27). In pine (5), deposition is much lower 1/4 mile from a stand than within the stand.

To the third group of studies belong those concerned with seasonal fluctuations in pollen frequency at a given station (hayfever counts). Since the source frequency is almost always unknown these data cannot be used in the study of dispersion distances.

To the fourth group of studies belong those of Schmidt (24), Dyakowska (9), Sutton (25), and Gregory (11). Schmidt used Stokes' law for the velocity of fall of small particles in a viscous fluid to calculate the velocity of fall of pollen grains. This law stresses the size and density of the grain and the viscosity and density of the air. His calculated rate of fall for Scotch pine pollen (5.3 centimeters per second) was not greatly different from the value later measured by Dyakowska (3.7 centimeters per second. He then derived a formula for limit of spread in which the distance traveled by a given proportion of the pollen released varies directly with wind velocity and a constant relating to air turbulence, and inversely with the viscosity of the air and the square of the rate of fall.

Dyakowska measured the actual rates of fall in still air of a large number of tree pollens. She then used Schmidt's formula to determine the limit of spread of these pollens. She calculated that in wind of 22 miles per hour 1 percent of the pollen should travel more than 0.4 mile for Abies pectinata (large pollen falling 38.7 centimeters per second), 46 miles for Scotch pine, and 135 miles for Salix caprea (small pollen falling 2.2 centimeters per second). The corresponding distance for Scotch pine as calculated by Schmidt was 22 miles. Both Schmidt and Dyakowska considered that rate of fall and wind velocity were most important in determining dispersion distance.

Gregory based his considerations mainly on Sutton's "eddy diffusivity" theory, according to which pollen is dispersed mainly as a result of air eddies of ever-increasing size rather than by wind of a constant direction. He considered deposition at any one point to be proportional to the pollen content of the air above that point and to be governed by an empirically determined deposition coefficient. This deposition coefficient depends upon rate of fall among other things but not in as direct a manner as postulated by Schmidt; his justification for this is that known rates of fall are negligible in comparison with the rates of vertical air movement and that rate of fall is the governing factor only after the pollen reaches a "capture zone" of still air near the ground. He considered wind direction--but not velocity--as important. Briefly stated, Gregory postulated that the deposition at any point varies directly as the amount of pollen liberated and as the deposition coefficient, and inversely as the square of the coefficient of diffusion and as the distance raised to a power (with limits of 1.24 and 2) relating to the air turbulence.

None of these workers has considered the height of the pollen source above the ground or the terrain and vegetation surrounding the source.

## METHODS

There are three ways in which dispersion of tree pollens might be studied so that the results would be directly applicable to natural conditions. First, pollen could be collected and liberated in the forest after the flowering season was past. However, this would necessitate the collection of very large quantities of pollen and very careful release to duplicate natural conditions. Second, seeds could be collected from trees at varying distances from a source tree carrying an easily identifiable marker gene. To do this, though, we would first have to locate the marker genes and breed them into suitable material. Third, the pollen of single trees could be marked with radioactive tracer elements. This would require much preliminary research on the physiology of mineral uptake in pollen.

For this study, therefore, it was decided to collect the pollen at varying distances from isolated source trees. This method has several limitations. Since it is practically impossible to differentiate pollens of some species--let alone trees within species--it was necessary to choose trees growing well away from others of the same species. Most of the trees were in the open rather than in a stand. Most were growing outside their native range under unusual terrain and weather conditions. The pollen counts were made near the ground rather than at flower level and included dead as well as viable pollen grains. It is conceivable that the counts at distant stations would have been much lower if only viable grains were counted.

These limitations affect the accuracy of the results. It would not be surprising to find that the experimentally determined distances of dispersion are in error by a factor of 2 or 3. However, in view of the general agreement between the results for different species and in two different regions and between some of the experimental results and Gregory's theoretical curves it is doubtful that they are in error by a factor of 5 or 10.

## POLLEN COLLECTION

Elm.--The source trees were a row of American elms (Ulmus americana)[4] on the west bank of the Wabash River in West Lafayette, Indiana. They were 60 to 70 feet tall. Pollen was collected along a traverse running east and west along U.S. Route 52, at right angles to the river. The river at this point is on the western side of the flood plain. To the east the land is flat and cultivated; to the west it rises for about $\frac{1}{2}$ mile to a level, cultivated upland approximately 150 feet above the river. Between the upland and the river was a beech-maple forest with an average height similar to that of the source trees. Pollen frequencies to the west of the source trees were probably reduced by the increasing elevation and by the reduction in wind velocity (due to the forest). There is believed to have been some contamination at stations to the east of the source trees by pollen from a group of American elms 1/4 mile south of the study transect.

The pollen was collected on vaseline-covered slides. These were exposed for 24-hour periods and were collected daily between 5 and 6 p.m. unless otherwise mentioned. The slides were exposed toward the south at a 45° angle, at a height of 2 feet above the ground. They were held in place in metal holders suspended one-half inch below curved pieces of metal about 6 inches square. All holders were located in the open away from obstructions. The covers gave nearly complete protection against light showers, but little against dust or heavy rains. On rainy days the slides were discarded. The microscope counts were made under low power (100x) in air; on each slide an area of 3.86 square centimeters was counted.

Poplar, ash, and Douglas-fir.--For the study of these species a transect (fig. 1) was established near the southwest limits of West Lafayette. East, northeast, and south of the transect the land was wooded or covered with houses and ornamental trees. To the west and north the land was open. In the area enclosed by Stations 24, 26, 27, and 32

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[4] FOR COMMON NAMES, THIS REPORT FOLLOWS THE U.S. FOREST SERVICE CHECK LIST OF THE NATIVE AND NATURALIZED TREES OF THE UNITED STATES INCLUDING ALASKA. 325 PP., 1944. FOR THE SAKE OF CONSISTENCY (SINCE SOME OF THE SPECIES STUDIED ARE NOT INCLUDED IN THE CHECK LIST), SCIENTIFIC NAMES USED FOLLOW REHDER, ALFRED. MANUAL OF CULTIVATED TREES AND SHRUBS, ED. 2, 996 PP., ILLUS. NEW YORK. 1940.

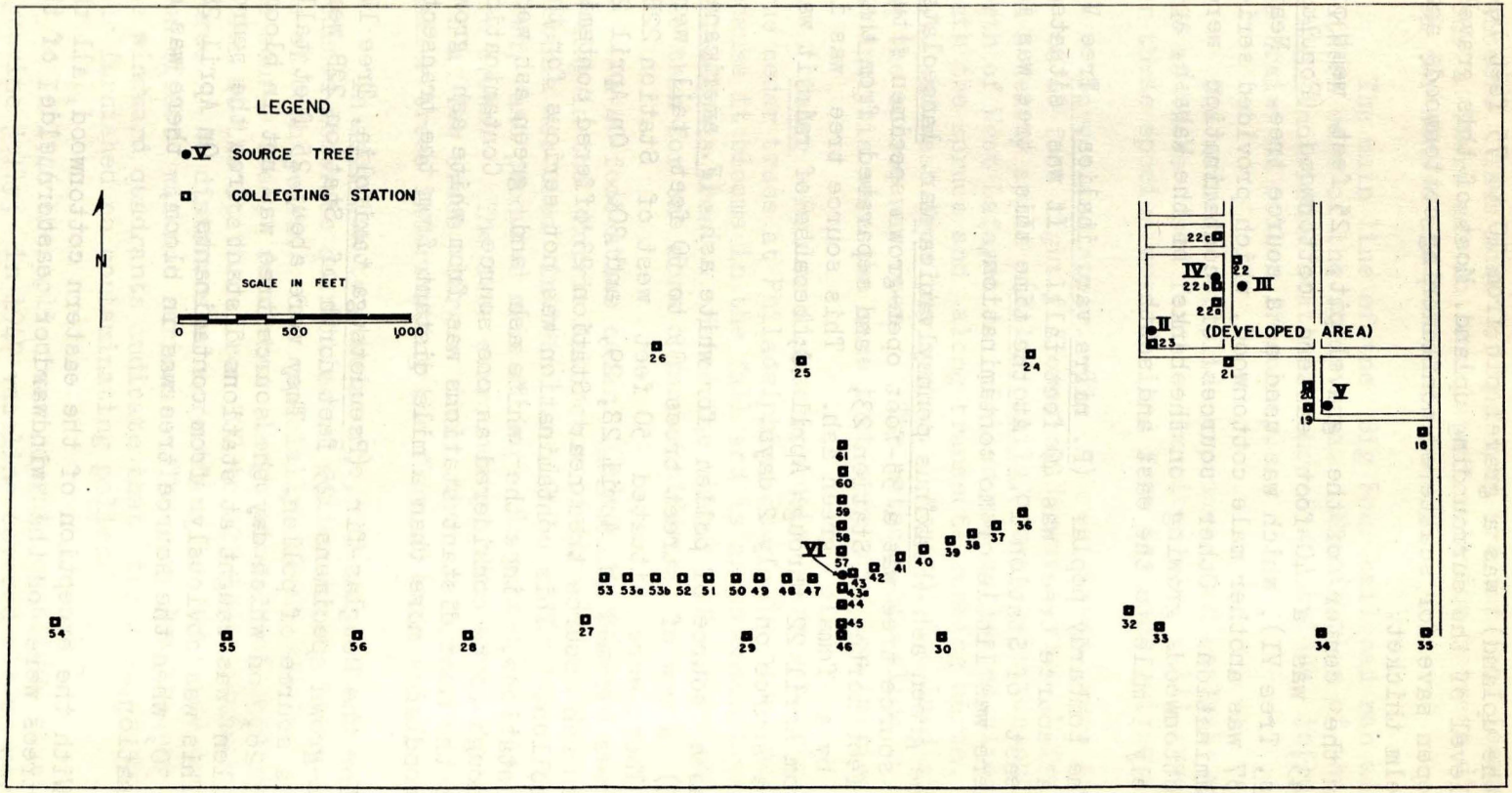


Figure 1.--Transect of the area used in collecting pollen of ash, poplar, and Douglas-fir. The built-up section is part of West Lafayette, Indiana.

(all on the upland) was a gravel pit from 10 to 75 feet below the level of the surrounding upland. Most of this gravel pit was open save for scattered nonflowering cottonwoods and a small elm thicket.

In the center of the gravel pit, 25 feet west of station 43, was a 40-foot eastern cottonwood (Populus deltoides, Tree VI), which was used as a source tree. Near Station 37 was another male cottonwood, which provided serious contamination. Other sources of contamination were large cottonwoods growing on the banks of the Wabash, approximately 1 mile to the east and south.

The Lombardy poplar (P. nigra var. italica, Tree V) used as a source tree was 40 feet tall. It was situated 50 feet east of Station 19. At the time this tree was in bloom there was little or no contamination.

The green ash (Fraxinus pennsylvanica var. lanceolata, Tree II) source tree was a 35-foot open-grown specimen situated 25 feet north of Station 23, and separated from that station by a female green ash. This source tree was in bloom from April 22 through April 28; because of rain it was used as a source on only 2 days.

As a source of pollen for white ash (F. americana, Tree III) a row of street trees 35 to 50 feet tall were used. They were situated 50 feet west of Station 22B. These trees bloomed on April 28, 29, and 30. On April 28 the green ash source tree near Station 23 offered contaminating pollen. This contamination was not serious for the distant stations, since the white ash and green ash were close enough to be considered as one source. Contamination found at the most distant stations was from white ash growing in woodlands more than a mile distant from the transect.

For the Douglas-fir (Pseudotsuga taxifolia, Tree IV) two open-grown specimens 25 feet north of Station 22B were used as a source of pollen. They were about 25 feet tall. On April 26, on which day the source tree was not in bloom, some pollen was caught at stations distant from the source tree. This was obviously from contaminants. On April 28, 29, and 30, when the source tree was in bloom, there was no contamination.

With the exception of the eastern cottonwood, all the source trees were on the windward or eastern side of the

transect. Thus most of the data are for the leeward stations. There was no consistent relation between direction from the source and pollen frequency.

The main line of the Big Four Railroad ran along the southern edge of the study area. Examination of the counts at the individual stations showed no obvious influence of the trains on pollen frequency.

The methods of slide exposure and analysis were the same as those used for the American elm. All frequencies for these species were derived from the same slides.

Spruce and apple.--The source trees were a row of 50- to 60-foot lightly flowering Norway spruce (Picea abies) and a nearby apple (Malus pumila) orchard situated 4 miles north of West Lafayette. Pollen was collected directly beneath the spruce and along transects running north, south, east, and west from the source. Most of the land surrounding the source was open. The methods of slide collection and analysis were the same that were used for American elm.

Cedar.--Pollen dispersion data were gathered for two true cedar trees at Philadelphia, Pa. The cedar was chosen because it blooms in the fall and is an uncommon tree in the Philadelphia area. Hence the chance of contamination was less than for the more common conifers.

A 40-foot Atlas cedar (Cedrus atlantica var. glauca) growing in the Morris Arboretum of the University of Pennsylvania was used in 1946 and 1947. This tree was open-grown, and produced male flowers in profusion over its entire crown. The area surrounding this tree is park-like, with a few trees larger than the source tree and many smaller trees interrupting the flow of air.

In addition to the source, three other Atlas cedars produced moderate quantities of pollen during the test periods of both years. One especially, about 300 feet south of the source tree, furnished large amounts of contaminating pollen at the stations from 300 to 425 feet southeast of the source. At distances of more than 500 feet the contamination effect was not serious. The very low frequencies in the windward quadrants indicate that trees other than these four furnished no contaminating pollen.

In 1946 the pollen was caught on slides covered with glycerine jelly; in 1947 vaseline-covered slides were used.

The vaseline proved more convenient and lasted better on days of light rain or dew. The slides were exposed horizontally 2 feet above the ground in heavy wire holders, unprotected from above. All slides were exposed in the open. An area of 1.86 square centimeters was counted on each slide. Groups of two or more touching grains were recorded as one grain.

The other source tree was a 45-foot cedar of Lebanon (C. libani) growing in the Morris Arboretum. The tree bloomed moderately. About two-thirds of the male strobili were in the upper third of the crown, and the remainder in the middle third. This tree bloomed after the other cedars had shed nearly all their pollen, so there was little chance of contamination. The pollen traps surrounding this tree were exposed for a 135-minute period, during which all branches bearing male strobili were thoroughly shaken. The shaking liberated about 50 percent of the pollen on the tree. The pollen traps were vaseline-covered slides exposed and counted as for the Atlas cedar.

Pinyon.--The pinyon (Pinus cembroides var. edulis) was chosen because it bloomed after all the other species of pine. As a source of pollen, a 25-foot, open-grown, profusely flowering tree in the Morris Arboretum was used. It is the only one of its kind in a radius of several miles. The area surrounding the source tree is for the most part open or covered with shrubs up to 10 feet tall. To the north are a few trees taller than the source tree. To the south, the land slopes gently uphill. Methods of slide exposure and analysis were the same as were used for the Atlas cedar in 1947.

## *CALCULATIONS*

### *Regression Equations & Neighborhood Size*

The "neighborhood" is the largest population within which breeding can be considered to take place at random. It does interbreed with its neighbors. The size of the unit is a measure of the amount of genetic differentiation that can be expected as a result of isolation by distance only.

Sewall Wright outlined the procedure for calculating the standard deviation of the distance of pollen dispersion

($\sigma_D$) and made sample calculations.[5] The data were fitted to the curve

$$(1) \qquad y = y_o e^{-kD}$$

which Bateman (3) found moderately satisfactory for wind-pollinated species. In this formula $y_o$ is the source frequency, y is the frequency at a given distance (D), and k is a constant relating to the decrease in dispersion rate with distance. Stated logarithmically the formula is

$$(2) \qquad \text{Log } y = \text{Log } y_o - (\text{Log}_{10} e)kD$$

The regression was calculated from the ordinary regression formula, using the average number of pollen grains at a station as the weight. The variance was $2/k^2$; so $\sigma_D$ was $\sqrt{2}/k$.

From the $\sigma_D$ the size of the effective population in a "neighborhood" (random breeding unit, panmictic unit) was calculated from the following formulae derived by S. Wright. In these formulae, N is the effective population size and d is the density of breeding individuals per linear foot of linearly continuous range or per square foot of areally continuous range.

For hermaphroditic populations with linearly continuous ranges (along a stream or lake shore) and equal dispersion of seed and pollen,

$$(3) \qquad N = 2\sqrt{\pi}\,\sigma_D d = 3.54\,\sigma_D d$$

For hermaphroditic populations with areally continuous ranges and equal dispersion of seed and pollen,

$$(4) \qquad N = 4\pi\,\sigma_D^2 d = 12.6\,\sigma_D^2 d$$

For hermaphroditic populations with linearly continuous ranges and only the pollen dispersed,

$$(5) \qquad N = \sqrt{2\pi}\,\sigma_D d = 2.51\,\sigma_D d$$

For hermaphroditic populations with areally continuous ranges and only the pollen dispersed,

$$(6) \qquad N = 2\pi\,\sigma_D^2 d = 6.28\,\sigma_D^2 d$$

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[5] PERSONAL COMMUNICATION, 1949.

Seed dispersion was usually taken as much less than pollen dispersion, or zero, to facilitate the calculations. Actually, there is no serious error in interpretation if the calculated value of N is twice or half its real value, because of the variations in N in nature.

For dioecious populations the formulae for the effective number of either male or female trees are the same as the formulae given above for equal dispersion of seed and pollen. The effective number of females is assumed equal to the effective number of males.

*Pollen Trajectories With Rate Of Fall & Wind Velocity The Controlling Factors*

From the rate of fall, the height at which the pollen is shed, and the horizontal rate of air movement during the period of fall, it is theoretically possible to determine the frequency distribution of pollen grains at varying distances from the source. Certain assumptions must be made. These are: (1) Horizontal wind velocity is not affected by height above ground; (2) horizontal wind velocity is not affected by barriers such as the pollen source tree; (3) there is no vertical air movement.

Theoretical pollen frequency distributions were calculated for the pollen of two species. For the calculations it was assumed that pollen was distributed uniformly over the tree from a height of 10 feet above the ground to the top of the tree. Wind velocities were taken from the actual weather records of days during the observation period. Rates of fall were taken from Dyakowska.

The first step in obtaining the theoretical frequency distribution of pollen-dispersion distances was to obtain frequency distributions of V (wind velocity in feet per second), H (height of the pollen above ground, in feet), and T (time in seconds to fall a given distance in feet). Then arbitrary class limits were established in the V, H, and T distributions so that the products of the class means equaled previously set class means in the dispersion-distance distribution. Next the proportions of the pollen occurring in each class in the V, H, and T distributions were determined from the actual distributions. The products of these proportions were determined separately for each

different combination of V, H, and T, and were summed for each product of V·H·T. These sums form the pollen-dispersion distribution.

Two of these theoretical pollen distributions are presented in figure 6. They were calculated as if all the pollen were distributed in a line downwind from the source.

## *WEATHER DATA*

The weather data for the studies in West Lafayette were obtained from the official U. S. Weather Bureau station in West Lafayette. This station was located atop a 3-story building near the transect used for ash, poplar, and Douglas-fir. The wind velocities were undoubtedly much higher than those found near the ground on the transect, but were probably similar to those found at treetop level.

The weather data for the studies in Philadelphia were obtained from the official U. S. Weather Bureau station in Philadelphia. This was situated in the downtown section, several miles from the study area. Because of a somewhat sheltered exposure of the anemometer, the recorded wind velocities were somewhat lower than the actual velocities. However, they were undoubtedly higher than wind velocities near the ground in the test area.

# RESULTS

## *ELM*

### *(Ulmus americana)*

Pollen was collected during four periods, April 2-6, April 7, April 12, and April 13, 1944. Daily minimum and daily maximum temperatures during this period varied from 23° to 44° F. and from 40° to 61°F. respectively; average daily wind velocity varied from 9 to 17 miles per hour.

Total numbers of pollen grains collected were 643, 934, 99, and 101 respectively for the four collection periods. By far the greatest number were collected on April 7,

the warmest and least windy day (44° F. minimum and 59° F. maximum temperature, 9 miles per hour average wind velocity) of the blooming period. Apparently little shock was needed to dislodge pollen from the weak-pedicelled flowers once the anthers were opened by high temperature. Average distance of dispersion was about the same on this day as on windier days.

At distances of 0, 500, 1100, 1700, 2100, 2700, and 5500 feet west of the source tree, pollen counts for the entire collection period were 941, 115, 152, 73, 26, 12, and 8 respectively (fig. 2). At distances of 700, 900, 2800,

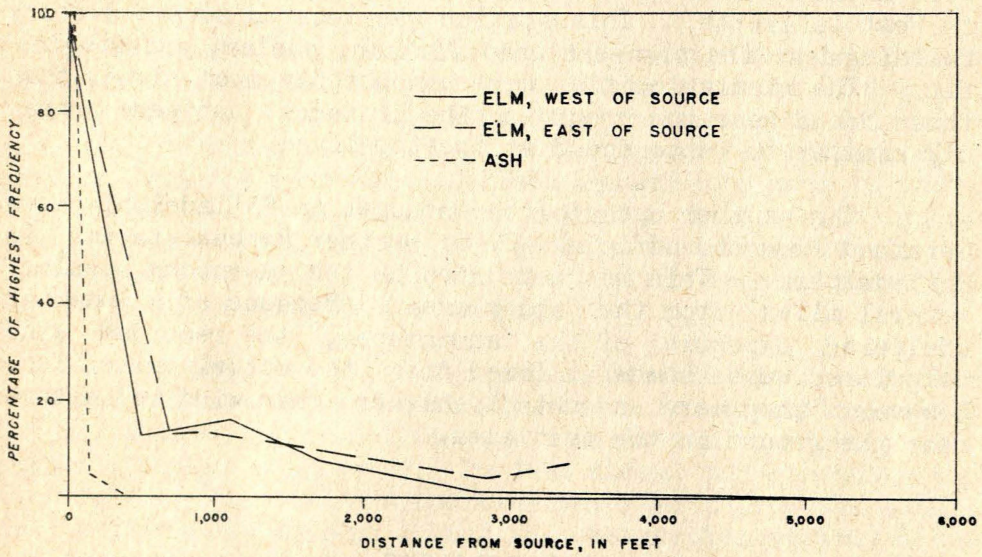


Figure 2.--Pollen-dispersion curves for American elm and white and green ash. The frequency of pollen decreases as distance from the source tree increases.

and 3400 feet east of the source tree the counts were 192, 129, 61, and 68 grains respectively. The lower counts to the west were due to the facts that there was little contamination from outside sources and that the land rose considerably from the source tree to the more distant stations. The direction of spread was not influenced greatly by average

wind direction of an entire day; slightly greater counts were obtained from the windward transects than from those to leeward.

Basing the calculations on counts for all days out to 5500 feet, the regression equation is

$$\text{Log } y = 2.640 - 0.0000882D$$

and $\sigma_D$ is 2200 feet. This figure may be overestimated by 2 or 3 times because of contamination. However, even allowing for contamination it is difficult to believe that the dispersion pattern for elm pollen is the same as that for pollen of the other species studied.

## *A S H*

*(Fraxinus americana, F. pennsylvanica var. lanceolata)*

The green ash source tree shed pollen on April 26, 1944, the white ash on April 26-30, 1944. Separate counts were made for each of the 4 days for nearly every station shown in figure 1.

The weather during the pollination period was warm; daily minimum and maximum temperatures varied from 38° to 52° F. and from 61° to 71° F. respectively. Average daily wind velocity varied from 9 to 20 miles per hour.

The highest daily count for white ash was obtained on the first day of the blooming period, which was relatively cool. There was not much difference in average dispersion distance between three days when the average wind velocity was 9 to 10 miles per hour and one day when the average wind velocity was 20 miles per hour.

The average wind direction was from the northeast on all days. Thus nearly all the counts were made from stations to leeward of the source trees. There was no constant relation between direction from source and relative count. Nor were there pronounced differences between the counts for different days or for different species.

If the counts for all days and both species are grouped according to distance from the source, the average counts per station per day at distances of 25, 50, 150, and 400 feet from the source are 2502, 1110, 110, and 2 grains

respectively (fig. 2). There was a very marked diminution of pollen frequency with increasing distance from the source.

Beyone 400 feet there was an increase in deposition although the counts were still very low compared to those near the source tree. Average counts per station per day were 5, 5, 9, 13, 6, and 4 grains at distances of 600-1000, 1100-2000, 2100-3000, 3100-4000, 4100-5000, and 5100-6000 feet respectively. This apparent increase beyond 400 feet was in all probability due to contamination from outside trees as there were several stands containing ash a mile or more distant from the study area. These stands, which were blooming at the same time, could easily have contributed many times the amount of pollen to the air that was contributed by the few source trees used.

In calculating $\sigma_D$ the average counts for all days for both species at stations from 25 to 400 feet were used; counts at more distant stations were considered due to contaminants. The regression equation is

$$\text{Log } y = 3.657 - 0.01116D$$

k is 0.02567 and $\sigma_D$ is 55 feet.

## *POPLAR*

*(Populus deltoides, P. nigra var. italica)*

Pollen counts were made for one day, April 22, 1944, for a single Lombardy poplar. On this particular day the native cottonwoods in the vicinity were not yet in bloom and the chances of contamination were very slight. At distances of 50, 100, 500, 900, 1400, 2500, 3200, 3300, and 4200 feet from the source, counts of 202, 8, 110, 38, 65, 8, 126, 125, and 44 grains respectively were obtained (fig. 3).

Counts of eastern cottonwood pollen were made for each of 4 days, April 26, 28, 29 and 30, 1944, during which a native cottonwood was in bloom. Nearly all the stations shown in figure 1 were included in the counts. The counts were highly variable from station to station and from day to day. There was essentially no correlation between direction of dispersion and wind direction. At distances of 25, 125, 250, 375, 500, 600-1000, 1100-2000, 2100-3000, and 3100-4000 feet, average counts of 146, 51, 74, 17, 33, 39, 20, 10, and

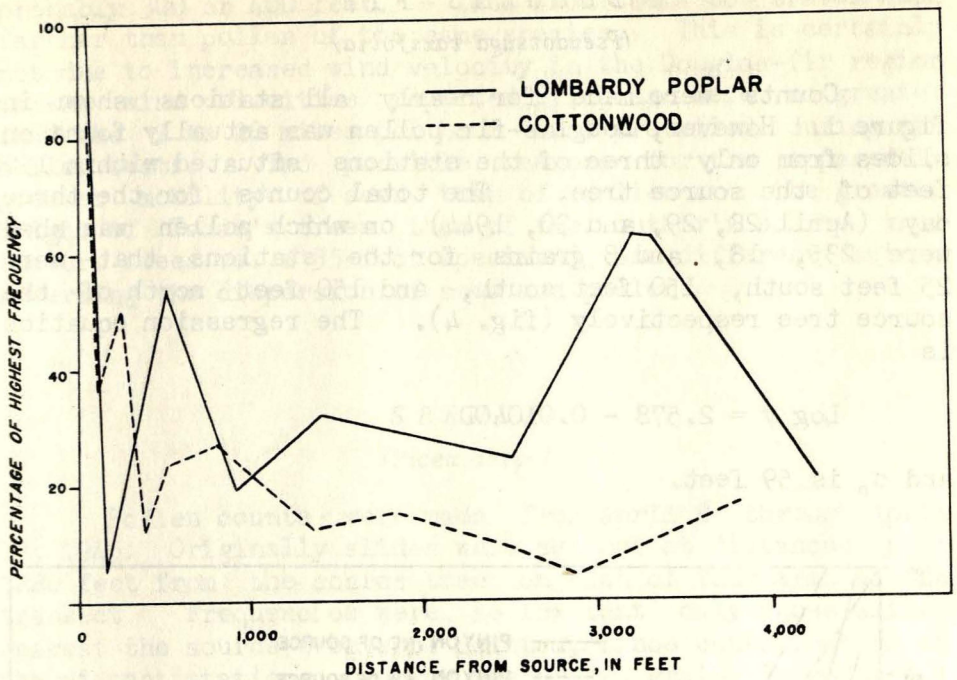


Figure 3.--Pollen-dispersion curves for Lombardy poplar and cottonwood.

25 grains per station per day were obtained. Flowering native cottonwoods along the Wabash River about a mile away may have contributed considerable contaminating pollen.

In neither case was there a pronounced decrease in pollen frequency (in comparison with the other species studied) with increasing distance from the source. True, the frequency was always highest nearest the source, but frequencies half as great were found several hundred feet away.

The lack of any regular decrease in pollen frequency makes the calculation of a value for $\sigma_D$ from the present data meaningless. The value of $\sigma_D$ must certainly be large, possibly in excess of the 4,000 feet included in the transects used.

## *DOUGLAS-FIR*

*(Pseudotsuga taxifolia)*

Counts were made for nearly all stations shown in figure 1. However, Douglas-fir pollen was actually found on slides from only three of the stations situated within 150 feet of the source tree. The total counts for the three days (April 28, 29, and 30, 1944) on which pollen was shed were 235, 18, and 3 grains for the stations that were 25 feet south, 150 feet south, and 150 feet north of the source tree respectively (fig. 4). The regression equation is

$$\text{Log } y = 2.578 - 0.01040D$$

and $\sigma_D$ is 59 feet.

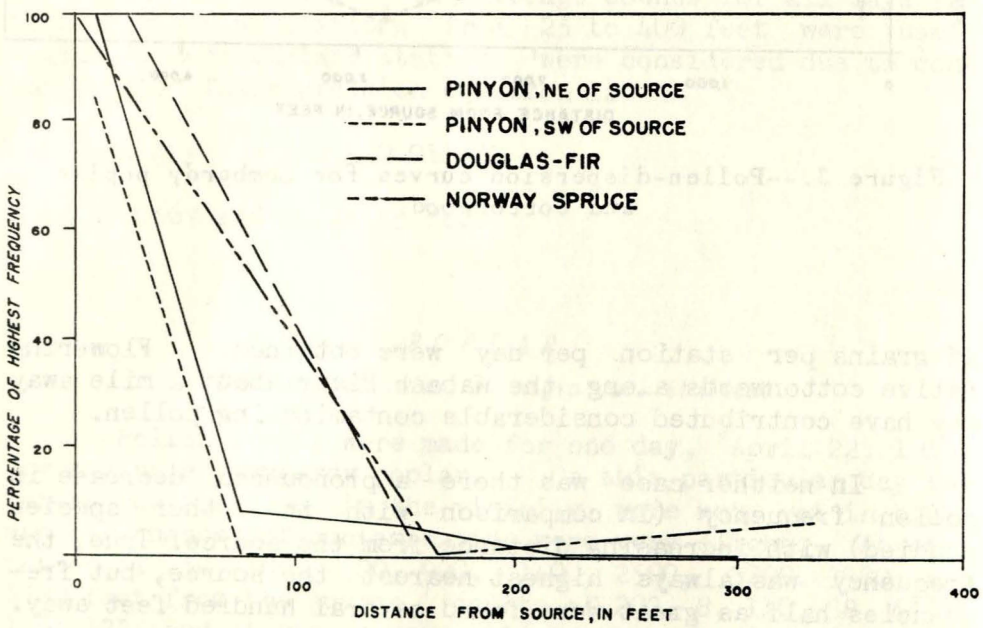


Figure 4.--Pollen-dispersion curves for pinyon, Douglas-fir, and Norway spruce.

Isaac (15) found that most of the Douglas-fir seed released from natural stands fell within 300 feet of the stand but that appreciable amounts were carried up to 2400 feet. The $\sigma_D$ for seed dispersion for Isaac's data is

probably 300 or 400 feet. Thus seed seems to travel much farther than pollen of the same species. This is certainly not due to increased wind velocity in the Douglas-fir region as the wind velocities reported by Isaac were no greater than the 9 to 20 miles per hour that prevailed during the pollen tests. Two possible reasons for the apparently greater mobility of seed than of pollen are the greater height of Isaac's trees than of the author's source tree (mature trees vs. a 35-foot specimen), and different factors governing the dispersion of seed and pollen.

## *SPRUCE*

### *(Picea abies)*

Pollen counts were made from April 8 through April 13, 1945. Originally slides were set out at distances up to 5280 feet from the source tree on each of four arms of the transect. Frequencies were so low that only those slides nearest the source tree were counted, since contamination at the distant stations by even one or two grains introduced a serious error. The average counts per station per day were 9.7, 0.1, and 0.7 respectively at distances of 0, 165, and 330 feet from the source (fig. 4). The regression equation is

$$\text{Log } y = 0.978 - 0.00359D$$

and $\sigma_D$ is 126 feet.

## *APPLE*

### *(Malus pumila)*

Counts of apple pollen made on the Norway spruce slides for the period from April 8 through April 11, 1945, showed average frequencies per station per day of 132, 1.2 and 2.0 respectively, at distances of 0, 165, and 330 feet from the source. Since apple is primarily insect-pollinated, a more rapid decrease in frequency might have been expected. The regression equation is

$$\text{Log } y = 2.111 - 0.00574D$$

and $\sigma_D$ is 107 feet.

## *PINYON*

*(Pinus cembroides var. edulis)*

The pinyon shed its pollen in mid-June, 1947, after all other pines had finished flowering. The source tree is the only flowering one of its species known in the Philadelphia area. Consequently there was no contamination.

The weather during the 3-day pollen-collection period was warm and humid, with minimum temperatures of 68° to 78° F., maximum temperatures of 85° to 93° F., and relative humidity at 1:30 p.m. from 68 to 79 percent. The average wind velocity was 7 to 8 miles per hour, with occasional gusts reaching 17 miles per hour. The total counts for all stations were 4668, 2775, and 1675 grains respectively for the first, second, and third days of the tests. The highest counts were obtained on the first day, which was slightly more windy and cooler than the other two days. Probably the reason for this is that most of the easily shed pollen was dislodged on the first day, leaving less for the rest of the blooming period.

Separate counts were made each day for each of 18 stations on transects running north, south, east, and west from the source tree. Although the average wind direction shifted from the south to the northwest between June 11 and 12, there was no corresponding shift in the pollen frequencies in the various transects. The relative frequencies at individual stations stayed fairly constant from one day to the next.

The highest frequencies were obtained from the northern and eastern quadrants, possibly because they were the leeward on two of the three days and were on the downhill side of the source tree and were relatively brushy. Especially at the more distant stations the counts on these transects were many times those obtained from the open southern and western transects (fig. 4).

The very rapid decrease in pollen deposition with increasing distance on all transects is shown in table 1. Every day, on each transect, the highest frequencies were obtained from the station nearest the source tree, with the next highest frequency usually occurring at the next nearest station.

Table 1.--Number of pollen grains collected at varying distances from pinyon source tree, June 1947

| Distance from source (feet) | Direction from source | | | | Total |
|---|---|---|---|---|---|
| | N | W | S | E | |
| 10 | 2,304 | 1,871 | 2,007 | 2,298 | 8,480 |
| 75 | 245 | 15 | 2 | 176 | 438 |
| 150 | 38 | 4 | 5 | 94 | 141 |
| 225 | 10 | 2 | 1 | -- | 13 |
| 300 | 14 | 3 | -- | 29 | 46 |

Using the totals for all days, the regression equation for pollen frequency at varying distances was

$$\text{Log } y = 4.0194 - 0.01118D$$

and $\sigma_D$ was 55 feet.

## *TRUE CEDAR*

*(Cedrus atlantica var. glauca, C. libani)*

The cedars used in this study are true cedars, which differ greatly in all respects from the numerous other genera that are commonly called cedars. They should not be confused with these other trees because of the similarity in name.

The blooming habits of the true cedars are peculiar. They bloom in the fall, a habit shared by few other temperate-zone trees. Their period of pollen shedding is spread over a period of 10 days or 2 weeks, even though the male strobili are mature and the microsporangia are open early in the blooming period. Most other forest trees shed their pollen in a period of one or a few days unless the blooming is interrupted by a period of cold or rain.

The pollen-shedding periods during which pollen-dispersion records were made for the Atlas cedar source tree were September 18 through October 2, 1946, and October 6

through October 17, 1947. The ranges in daily averages for temperature and wind velocity during the two pollination periods are shown in the following tabulation

RANGES DURING ENTIRE POLLINATION PERIOD

| Pollination period | Daily minimum temperature | Daily maximum temperature | Daily average wind velocity |
|---|---|---|---|
| | °F. | °F. | M.p.h. |
| 1946 | 46-69 | 55-91 | 4.0-10.5 |
| 1947 | 50-64 | 67-80 | 4.2- 9.2 |

VALUES FOR THE DAY WITH THE GREATEST POLLEN FREQUENCY

| | | | |
|---|---|---|---|
| 1946 | 46 | 55 | 9.3 |
| 1947 | 57 | 68 | 9.2 |

The days with the highest pollen counts were the coldest, next-to-windiest of the entire blooming period in 1946, and the next-to-coldest, windiest day of the entire blooming period in 1947. The actual counts obtained were influenced by the amount of pollen left on the tree for dispersion. Warm days are needed to open the microsporangia, but the male strobili in Cedrus are erect and stiff (much stiffer than in pine or spruce), and very vigorous shaking is needed to dislodge all the pollen on a branch. Evidently the amount of shaking necessary can be provided only by wind of greater-than-average velocity. Hence the high counts on cold, windy days. Scamoni (23) has pointed out that the same thing is true in Scotch pine; however in that species less shock is needed.

A slight (probably not significant) inverse correlation between wind velocity and distance of dispersion was noted in the 1946 data. September 30 through October 2 were the windiest days of the observation period. Yet on these days stations more distant than 20 feet from the source tree in the windward quadrants yielded only 3 pollen grains (of 1,540 grains collected on those days), and counts at the distant stations in the leeward quadrant were a little less than average for the entire period. On the other hand, counts at the more distant stations were greater than average during the less windy (average wind velocities were one-half to two-thirds as great) period of September 18-29. Also, dispersion distances were greater in 1947 than in 1946 in spite of lower wind velocities on the days of high counts.

There was a good correlation between average wind direction and direction of pollen dispersion. Thus on September 22, 23, 30, and October 1, and 2, 1946, more than 99 percent of the pollen was obtained in the leeward quadrants. The correlation would probably be better if all the numerous changes in wind direction during a day were taken into account.

There seemed to be a correlation between topography and direction of pollen dispersion. The land sloped gently downward to the south of the source tree whereas to the north and northwest it rose more steeply. On nearly every day the counts were much less at the uphill stations than at equidistant stations downhill from the source tree. During the 2 years an average of 1.0 grains per station were caught at a distance of 700 feet in the uphill quadrants and 10.6 grains per station at the same distance in the downhill quadrants. Of course most of this difference was due to the prevailing wind direction. However, even on days when the wind was from the downhill side the counts at the uphill stations were lower than from comparable downhill stations.

The frequencies at varying distances from the source tree (fig. 5) are given in table 2. The data for all days

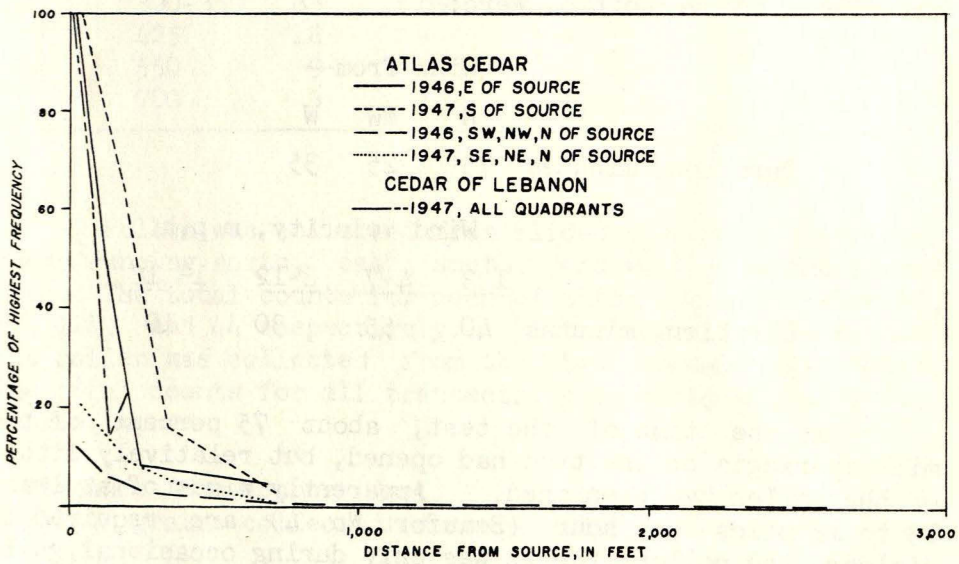


Figure 5.--Pollen-dispersion curves for Atlas cedar and Cedar of Lebanon.

were grouped in compiling the table although there was considerable day-to-day variation in the counts on the same transect. Thus nearly all the grains for the SW, NW, and N transects during 1946 were obtained during the period September 18-29 although from the SE transect appreciable numbers of grains were obtained every day during the observation period. As noted previously, this day-to-day variation was probably due to changes in wind direction.

Whether we consider the daily counts or the totals given in table 2 there was a consistent decrease in pollen frequency with increasing distance from the source on each transect. However, there was an exception. In 1946 a slide was kept a few inches directly below a heavily pollinating branch (distance 1 foot from source in table 2). Although the counts on this slide were always high they were exceeded each day by the counts at one or more of the stations situated 20 or 120 feet from the source tree.

In using the Lebanon cedar as a source tree, a short observation period of 135 minutes was used and the pollen was shaken loose in order that all the details of the pollen dispersion could be noted. During the test, wind direction and approximate velocity on the Beaufort scale were recorded at 5-minute intervals by observing the movements of pollen and branches. The elapsed times with winds of different directions and velocities were:

| | Wind from-- | | |
|---|---|---|---|
| | N | NW | W |
| Duration, minutes | 75 | 25 | 35 |

| | Wind velocity, m.p.h. | | | |
|---|---|---|---|---|
| | 1-3 | 4-7 | 8-12 | 13-18 |
| Duration, minutes | 40 | 55 | 30 | 10 |

At the time of the test, about 75 percent of the microsporangia on the tree had opened, but relatively little of the pollen had been shed. Apparently winds of at least 13 to 18 miles per hour (Beaufort No. 4) are required to dislodge the pollen, for it was only during occasional gusts of this velocity that pollen was visibly loosened except by the shaking. Sometimes a dozen vigorous shakes failed to loosen all the pollen.

Table 2.--Number of pollen grains collected at varying distances from Atlas cedar source tree

1946 COLLECTIONS

| Distance from source (feet) | Direction from source (magnetic azimuth) | | | | Average |
|---|---|---|---|---|---|
| | 108° | 230° | 294° | 4° | |
| 1 | -- | 275 | -- | -- | 275 |
| 20 | 829 | 107 | -- | -- | 468 |
| 120 | 491 | 52 | 81 | 16 | 160 |
| 240 | 64 | 4 | 25 | 53 | 36 |
| 690 | 36 | 0 | 2 | 2 | 10 |
| 1,200 | -- | 4 | -- | -- | 4 |
| 2,600 | -- | -- | 0 | -- | 0 |
| | 1947 COLLECTIONS | | | | |
| | 112° | 192° | 342° | 52° | |
| 40 | 82 | 440 | 87 | 105 | 178 |
| 125 | 95 | -- | -- | -- | 95 |
| 175 | -- | 295 | 10 | 36 | 114 |
| 300-350 | 85 | 69 | 0 | 9 | 40 |
| 425 | 18 | -- | -- | -- | 18 |
| 550 | 9 | -- | -- | -- | 9 |
| 700 | 3 | 12 | 0 | 2 | 4 |

Pollen was collected from slides placed on four transects running north, east, south, and west from the source tree. The total counts for each of these transects were 36, 57, 124, and 44 respectively. Approximately 69 percent of the pollen was collected from the two leeward quadrants. The total counts for all transects, grouped by distance from source, were:

| Distance from source (feet) | 15 | 75 | 135 | 195 |
|---|---|---|---|---|
| Pollen grains collected (number) | 125 | 88 | 18 | 30 |

The highest count was obtained at the 15-foot stations in all transects except the southern (leeward) one, where the highest count was obtained at the 75-foot station. The rate

of pollen decrease with increasing distance is similar to that found for the Atlas cedar.

There are three other flowering trees of Atlas cedar in the Morris Arboretum that might have furnished contaminating pollen. They are so located that their pollen would have most influenced the counts in the southeast and southern quadrants, which did indeed show the highest counts. It is probable that they furnished no more than one-third or one-half of the pollen counted at stations 200 to 400 feet from the source tree in these quadrants, and negligible amounts in other quadrants. Because of difference in blooming times they probably furnished no contamination in the Lebanon cedar test. There are other true cedar trees in the vicinity but the low counts at distant stations in the windward quadrants indicate that they offered no contaminating pollen.

The values of $\sigma_b$ were calculated separately for the 1946 Atlas cedar data, for the 1947 Atlas cedar data, and for the cedar of Lebanon data. The respective regression equations are:

$$\text{Log } y = 2.6418 - 0.002571D$$
$$\text{Log } y = 2.9207 - 0.002578D$$
$$\text{Log } y = 2.175 - 0.004046D$$

and the values of $\sigma_D$ are 238 feet, 238 feet, and 145 feet.

## FACTORS THAT INFLUENCE DISPERSION DISTANCE

### *WIND VELOCITY & DIRECTION*

Dyakowska and Schmidt laid great stress upon the velocity of the wind. Sutton and Gregory, however, disregarded wind velocity in making their calculations of pollen dispersion.

Several facts from the author's study support the view that average wind velocity is unimportant. In the elm study the dispersion distances were greater on April 7, the least windy day of the observation period, than on other

days. Dispersion distances for ash and Douglas-fir were about the same on April 30, 1944, as on other days when the average wind velocity was only half as great. In Atlas cedar, dispersion distances were greater in 1947 than in 1946 and in September 18-29, 1946, than in September 30-October 2, 1946--although in each case the last named period was the windiest.

The curves shown in figure 6 were calculated to test the "trajectory" concept, that the travel distance of a pollen grain could be calculated from its rate of fall and the succession of wind velocities to which it was subjected. There is no correspondence between the actual and theoretical curves indicating that wind velocity can in fact be disregarded. (These theoretical curves are not subject to the limitations attending average-velocity calculations, because they are based on all the actual velocities occurring during a day).

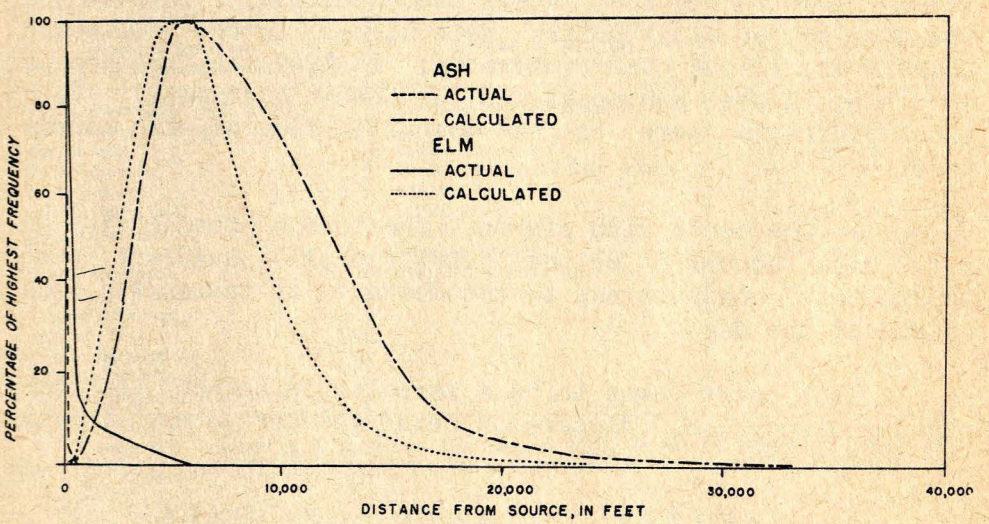


Figure 6.--Relation between actual and theoretical dispersion curves for elm and ash. For the theoretical curves (calculated according to the ideas of Schmidt and Dyakowska), the pollen grain was treated as an individual body subject to the action of wind and gravity. Actual conditions indicate that other factors are more important than wind and gravity.

Wind velocity did have an important bearing on the amount of pollen that was dispersed by Atlas cedar. The male strobili are erect and so stiff that little pollen is shed unless the branches are shaken by strong winds. This is also true in Pinus sylvestris (23) and probably in other conifers.

Wind direction had an important bearing on the dispersion patterns. With Douglas-fir, Atlas cedar, Lebanon cedar, and pinyon (2 days out of 3) the highest pollen counts were made to the leeward of the source tree. Since there was some dispersion to the windward of the source trees, this correlation was not perfect, due to (1) the influence of irregularities in the land surface, and (2) the eddies in the atmosphere and variations from "average" wind direction over a period of a day.

## *TOPOGRAPHY OF THE LAND*

In the elm studies, greater distance dispersion was noted to the east of the source trees, where the land was level, than to the west where the land rose. In 1946 the frequencies of cedar pollen were higher in the southeast than in any of the other quadrants; in 1947 the frequencies were high in the southeast and southwest quadrants. Both these quadrants were on the downhill side of the source tree.

In the tests with pinyon, the lowest frequencies on all 3 days occurred on the south (uphill) quadrant even though this quadrant was to the leeward of the source tree on one of the days.

Thus there seems to be a correlation between topography and dispersion, dispersion being greater downhill from the source tree.

## *DIAMETER & RATE OF FALL OF POLLEN GRAINS*

Schmidt and Dyakowska and others have assumed that rate of fall is a major factor governing dispersion distances. Doyle and Kane (8), Erdtman (10), and others have pointed out that sacs of pine, spruce, and Cedrus pollen seem to be much less useful in promoting buoyancy of the pollen in the air than in orienting the pollen grain in the female strobilis. On the other hand, Sutton and Gregory

reason that the rate of fall of most pollen grains is so slight that gravity becomes effective in deposition only after the grains are brought near the ground by eddies in the atmosphere.

In table 3 the plants used in this and other studies are listed in approximate order of dispersion distance, diameter, and rate of fall of their pollen grains. Spruce, ash, and pine are among the species with the smallest dispersion distances and the most rapid rates of fall, while the poplars, elms, and hazel have large dispersion distances and slow rates of fall. Thus, there appears to be some correlation between increasing dispersion distance and decreasing rate of fall, although not so great as postulated by Dyakowska. The generally higher counts downhill from the source trees also indicate that rate of fall is a factor in dispersion.

Table 3.--Comparison of pollen of various plants in regard to dispersion distance, size of pollen grains, and rate of fall in still air[1]

| Dispersion distance, least to greatest ($\sigma_g$ of 55 to thousands of feet) | Diameter of pollen grain, largest to smallest (100$\mu$ to 25$\mu$) | Rate of fall, highest to lowest (6.8 to 2.9 cm/sec.) |
|---|---|---|
| Pinus cembroides var. edulis | Pseudotsuga taxifolia | Picea excelsa |
| Pseudotsuga taxifolia | Picea excelsa | Secale cereale |
| Cedrus spp. | Cedrus deodara | Fraxinus spp. |
| Picea excelsa | Pinus cembroides var. edulis | Pinus cembra |
| Fraxinus spp. | Juglans regia | Populus spp. |
| Corylus avellana | Ulmus scabra | Ulmus glabra |
| Juglans regia | Secale cereale | Dactylis glomerata |
| Cotton | Populus tremula | Corylus avellana |
| Ulmus americana | Fraxinus americana | |
| Cocksfoot (Dactylis?) | Corylus avellana | |
| Phleum pratense | | |
| Lolium | | |
| Secale cereale | | |
| Populus deltoides | | |
| Populus nigra var. italica | | |

[1] Data from Gregory (11), Dyakowska (9), Erdtman (10), Jensen and Bøgh (16), Brown (4), Pope et al (21), Wood (27), Rempe (22), and the author's study.

## *TURBULENCE OF THE ATMOSPHERE*

Gregory pictures the eddies in the atmosphere as facilitating both dispersion and deposition of pollen. At the surface of the earth there is a relatively thin layer of calm air within which the force of gravity and electrostatic forces are free to act in causing the pollen to fall to

earth. Above this layer the air is in constant motion, both horizontally and vertically. The horizontal air movement is great enough at nearly all times to carry pollen consider-

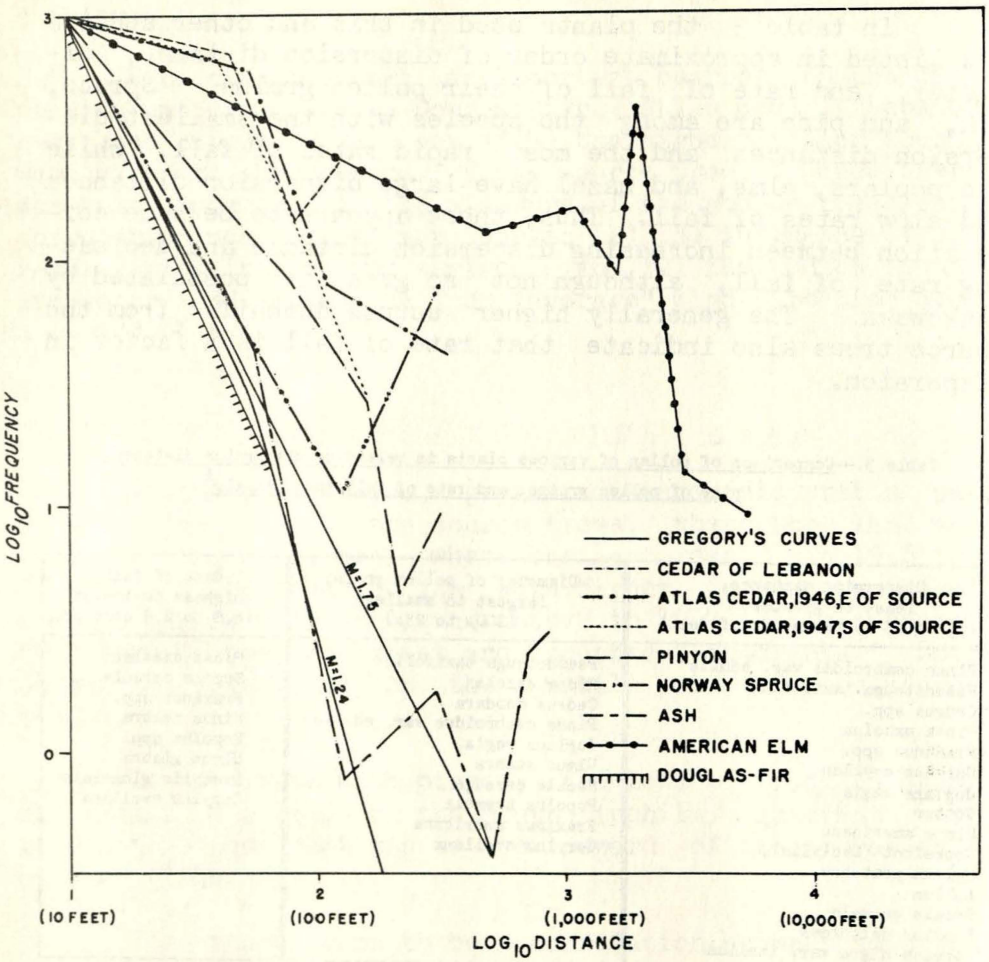


Figure 7.--Relation between actual dispersion curves for various species and theoretical dispersion curves based on Gregory's deposition coefficient (p = 0.05). In Gregory's calculations the turbulence of the atmosphere is deemed of great importance and rate of fall in still air of minor importance. The relatively good fit of the Douglas-fir, spruce, and ash curves indicates that Gregory's hypothesis is essentially true. However, the very real differences among curves for different species show that rate of fall in still air cannot be dismissed entirely.

able distances. Updrafts tend to counteract the slight downward movement due to gravity and to keep the pollen in the air indefinitely. Downdrafts carry the pollen down where it may be "captured" by the layer of calm air. According to this view the amount of deposition at any one point is proportional to the density of the pollen cloud above that point.

Bateman (3) found that Gregory's curves fit Jensen and Bøgh's data very well.

Figure 7 was drawn to test Gregory's hypothesis with the author's data. There is a good fit between the actual curves for Douglas-fir, ash, and spruce and Gregory's curve ($m = 1.75$, $p = 0.05$). But the actual curves for cedar, elm, and poplar (not shown) do not fit Gregory's curves. Even if we assume no deposition ($p = 0$), the curve (not shown) of number of grains passing over a unit area is still steeper than the pinyon curve. The discrepancy in elm and cottonwood may be due in part to contamination, but this is hardly so in cedar and pinyon. The longer-than-expected dispersion distances for these species indicate that the trajectory hypothesis may be operative under certain conditions (such as very low turbulence, relatively high pollen source, stations near source).

## *HEIGHT OF POLLEN SOURCE*

Under the trajectory hypothesis, the higher the pollen source the greater the expected dispersion distances. When comparing forest vegetation with grassland vegetation under Gregory's hypothesis the reverse might be true, as the forest provides a relatively thicker layer of still air to facilitate pollen deposition than does an open field.

These experiments provide only indirect evidence of the influence of height of pollen source. The dispersion distance was greater on the downhill side of the cedar. An examination of the first column in table 3 shows that the herbs studied have shorter dispersion distances than do most of the trees listed. Because of differences in methodology, land configuration, and species this trend cannot be taken at face value.

# POLLEN DISPERSION & RACE FORMATION

Briefly stated, the formation of a new race or species by the accumulation of a number of micromutations has been postulated as follows (7, 14, 17):

Recurrent mutations provide a source of variation on which selection can work. Selection pressure causes the frequencies of certain genes in the population to change or the make-up of certain gene complexes to shift. In the absence of isolating factors, selection may cause the entire population to shift toward a new genetic equilibrium and the population may be differentiated in time (i.e., populations following each other in geologic strata will be composed of different species); but at any one time the population will consist of only one race or species. In the presence of isolating barriers, selection may cause spatial differentiation as well as differentiation in time. In the view of Mayr (17) isolating barriers must be geographic; ecological races will be formed only if there is a spatial separation between the habitats in which the races are to be formed. This picture of raciation is believed to be a common one (but not the only one) in plants.

If a tree species has two separate ranges separated by hundreds of miles, and perhaps differing by 10° F. in average winter temperature, natural selection is perfectly free to operate and to produce a hardy race and a tender race. If however, the species is spread continuously up and down one mountain, the races are not so likely to form even though the average winter temperatures in two portions of the range differ by more than 10° F. Pollen from the top of the mountain will go downhill, carrying with it genes for hardiness (and vice versa); the next generation the same thing will happen. At any particular time the weather will kill the trees not adapted to a certain portion of the mountain but in the next one, two, or several generations there will be an influx of genes from other portions of the range. There can be no continuing effect toward splitting the species apart such as is possible if there is a gap in the range.

Under the following conditions an actual gap in the population is not necessary for raciation to occur. If the population is sparse enough, gene interchange can be so

slowed down that selection plays a dominant role. Or, if the population is dense but pollen and seed move only a few feet per generation, gene interchange is slowed down. If the population is spread from Maine to Florida it may take so many generations for the "cold" Maine genes to reach Florida that "cold" and "warm" races are formed in spite of the continued migration.

The investigations of S. Wright (30, 31, 32) offer a means by which we can study the possibilities of race formation in actual populations. Wright's models are of necessity fairly simple, with the density and mobility of the organisms assumed to be similar throughout the population. In these models he has had to ignore selection pressure (which is covered thoroughly in several of his earlier publications) and to concentrate on random gene fixation due to various degrees of in-breeding. Considering selection pressure and differences in population density from one portion of the range to the other does of course modify the conclusions based on the models.

Briefly, we need data on pollen dispersion, seed dispersion, and density of the breeding population in order to translate Wright's models into actual forest. To simplify the calculations, seed dispersion has been taken as zero; the results are not greatly in error (see formulae 3 to 6) if the seed travels a small distance compared with the pollen. The farther the pollen is dispersed and the more dense the population, the larger is the random breeding unit and the fewer are the chances for gene fixation within any given distance.

All these measurements and calculations are quite useless if we accept the view taken by some authors that one pollen grain or seed traveling over a long distance is sufficient to bring two races or species together. Whether or not this happens will depend on the value of the long-distance dispersion rate. For example, for large subpopulations (N = 1,000) a long-distance dispersion rate of less than 1/4 N will permit differentiation, as will a rate of 1/30 N for small subpopulations (where N = 10). However, where the long-distance dispersion rates are greater than these critical values the subpopulations will not differentiate (31).

In preparing the following estimates as to the amount of differentiation probable in various groups, neighborhood size has been derived from the pollen-dispersion data (see

"Results"). The necessary assumptions with regard to population density and continuity of range are believed to be reasonable. The effects of selection pressure have been neglected in these examples; consideration of selection pressure increases the probability of raciation in any given circumstances.

Poplar.--The cottonwoods usually have linearly continuous (riverbottom) ranges, occur in pure stands, and are dioecious. Assuming a $\sigma_D$ of 1,000 feet (low estimate), 25 flowering trees per acre, and a range 200 feet wide, the neighborhood has an effective size (from formula 3) of

$$N = 2\sqrt{\pi}\,\sigma_D d = \frac{3.54(1000)(25)(200)}{43560} = 200 \text{ trees}$$

Only over many hundreds of miles of continuous range would different alleles approach fixation (31), and there would be little or no local raciation. With a population density of 10 the neighborhood would contain 160 trees, a value which would permit some differentiation of large subpopulations.

Elm.--American elm is essentially a riverbottom (linear range), hermaphroditic species with light seeds. Assuming linear continuity of range, no seed dispersion, a fruiting population 200 feet wide containing 10 trees per acre, and a $\sigma_D$ of 2,200 feet, the neighborhood has an effective size of about 250 trees, using formula 5. Assuming areal continuity of range, the neighborhood size (using formula 6) is 6,970 trees. With linear continuity we should expect differentiation over a space of a few hundred miles. With areal continuity we should not expect differentiation unless the population density is unbelievably small. At present, elm in the Midwest occurs in woodlot "islands," but these "islands" are so close together that they form an essentially continuous range.

Ash.--Green ash is primarily a riverbottom, dioecious species usually occurring in mixed stands. The seeds are relatively heavy, not used much by wildlife, and probably dispersed only short distances. Assuming linear continuity of range, $\sigma_D$ of 75 feet, 10 trees per acre (5 male, 5 female) and a range about 200 feet wide, the effective size of the neighborhood (using formula 3) is 12 trees (both sexes).

White ash is primarily an upland, dioecious species occurring in mixed stands, rarely with large numbers of fruiting trees per acre. Assuming areal continuity, $\sigma_D$ of 75 feet, and 10 trees per acre, the effective population size of the neighborhood (using formula 4) is 16 trees (both sexes). If the larger figure of 154 feet for $\sigma_D$ is used the neighborhood sizes for green ash and white ash are doubled and quadrupled respectively.

With linear continuity and the lower value for $\sigma_D$, we may expect random fixation of genes within the limits of a few miles (31). There should be considerable differentiation of both local and geographic races in both species. The occurrence of polyploidy in the white ash (26) further increases the possibilities of racial differentiation. Geographic progeny tests (19, 28, 29) show that well-differentiated geographic races or clines do occur within both species, and that in certain instances there are heritable differences between progenies of the same locality, which might mean the presence of local races.

Douglas-fir.--The species is widespread and hermaphroditic, occurring mixed or in pure stands, usually in large numbers. Assuming areal continuity, $\sigma_D$ of 59 feet, 25 trees per acre, the effective size of the neighborhood (using formula 6) is 25 trees.

However, Isaac's (15) data indicate a much larger value of $\sigma_D$ for seed dispersion. Using a value of 300 for $\sigma_D$, the neighborhood contains about 600 trees. With this size neighborhood there should be little racial differentiation within continuous tracts of timber.

The species is not continuous over its entire range. Mountain tops, lowlands, and bodies of water make numerous gaps which the species does not ordinarily cross. A gap of 2 miles seems sufficient to keep long-distance pollen and seed transport below the critical values. Munger (20) found well-defined geographic (but not local) races in the species.

For the interior population with shorter trees, lower population densities, more gaps in the range, and probably shorter seed-dispersion distances, the size of the neighborhood probably decreases toward the 25 trees obtained from the pollen-dispersion data. In this region the chances for race formation should be greater than along the coast, and local differentiation should be possible in some instances.

Pinyon.--The species is hermaphroditic and grows in low-density stands toward the lower edge of the timbered zone in the Southwest. Over rather small areas the range is areally continuous. Between these areas are small to large gaps (mountains, lowlands), many of which are effective in stopping the exchange of pollen and seeds. The effects of long-range transport in swamping local differentiation will be minimized because of the relatively small size of the local subpopulations. Thus each of these "islands" of pinyon can differentiate rapidly from its neighbors. That raciation has occurred is indicated by the fact that there are four geographic varieties of P. cembroides that are so well defined that they are sometimes regarded as distinct species.

Assuming areal continuity of range within a locality, 25 trees per acre, $\sigma_D$ of 55 feet, and no seed dispersion, the neighborhood is calculated from formula 6 to contain 11 trees. With such a small size considerable differentiation should occur within a locality as well as between geographic regions.

Cedar.--Atlas cedar in Morocco forms pure, open stands not unlike our own ponderosa pine stands of the West (13). The average stand contains about 25 trees per acre 12 inches and over in diameter. Assuming hermaphroditic, areally continuous populations, and no seed dispersion, and using formula 6 with our 1946 data on Atlas cedar, we find the neighborhood contains 120 trees. Using our 1947 data on Atlas cedar, we get a neighborhood of 207 trees; using Lebanon cedar data, 80 trees. With a neighborhood of 200 or less trees there can be a moderate amount of random differentiation among large subpopulations and among neighborhoods. With isolating strips of 1,500 or 2,000 feet between stands, considerable differentiation should occur. That raciation has occurred in Lebanon cedar is indicated by the fact that there are in the Northeast seed-propagated strains of this species (which has a relatively small natural range) that differ markedly in their hardiness.

Groups of plants other than those mentioned in the above examples give evidence both in support of and contradiction to the thesis that isolation and population numbers have played a major role in raciation and speciation. In support of this view are the many more races and species formed in the discontinuous populations of the West and in California in particular, the relative absence (except in

ponderosa pine) of published data on soil and altitudinal races (as against geographic-races) of trees. Contradicting the thesis is the fact that many uncommon species (butternut, blue ash) seem no more variable racially than are species with dense populations.

## SUMMARY


Pollen counts from various tree species were made on microscope slides covered with vaseline or glycerine jelly set out near the ground at varying distances from isolated source trees. In all the tests save one pollen-shedding was effected by natural shaking by the wind. Wind velocities varied from 5 to 20 miles per hour during the tests. The tests were conducted in level or gently rolling areas covered moderately by shade trees. The source trees used varied from 25 to 60 feet tall.

In American elm the pollen frequencies at 2,000 to 3,000 feet were 1 to 7 percent of the source frequency. The $\sigma_D$ of dispersion distance was large--probably a few thousand feet.

Ash pollen counts were exceedingly high near the source, but fell off rapidly to relative frequencies of less than 10 percent beyond 150 feet. The $\sigma_D$ is about 100 to 150 feet.

Douglas-fir pollen has a short average dispersion distance. No grains were found beyond 150 feet from the source tree. The $\sigma_D$ was found to be about 60 feet.

In Norway spruce and apple respectively, the frequencies at 330 feet were about 7 and 2 percent of the source frequencies. $\sigma_D$ was about 100 feet for both species.

The $\sigma_D$ of poplar pollen dispersion is probably in excess of 4,000 feet; there was no sharp diminution in amount of pollen with increasing distance.

Cedrus pollen dispersion diminished rapidly and regularly with increasing distance from the source. The frequencies at 700 feet were 4 percent or less of the source frequencies. The $\sigma_D$ was about 200 feet. Little pollen travelled uphill or against the wind.

Pinyon pollen travelled only short distances, the frequencies at 300 feet being 1 percent of the source frequencies. The $\sigma_D$ was 55 feet.

In Cedrus, pollen-shedding was greatest on cold, windy days. In the other species it was greatest on warm days.

In most cases pollen counts were much greater to the leeward than to the windward of the source trees, but pollen traveled as far or slightly farther during relatively calm periods than during windy periods. With one exception (ash) the species with shorter dispersion distances were those that have larger pollen grains and more rapid rates of fall. The experiments provided little data on the effects on dispersion patterns of air turbulence, height of pollen source, and topography of the land.

Of the various proposed theories of pollen dispersion, that of Gregory, in which air turbulence is stressed, best fits the observed data, although there are unexplained discrepancies.

The application of the results to race formation in trees are discussed. In Douglas-fir, Cedrus, ash, pinyon, and Norway spruce, pollen dispersion is sufficiently limited to permit genetic differentiation, expecially in regions where the population density is low.

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